Giant stem tetrapod was apex predator in Gondwanan late Palaeozoic ice age

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Current hypotheses of early tetrapod evolution posit close ecological and biogeographic ties to the extensive coal-producing wetlands of the Carboniferous palaeoequator with rapid replacement of archaic tetrapod groups by relatives of modern amniotes and lissamphibians in the late Carboniferous (about 307 million years ago). These hypotheses draw on a tetrapod fossil record that is almost entirely restricted to palaeoequatorial Pangea (Laurussia)[1,2]. Here we describe a new giant stem tetrapod, *Gaiasia jennyae*, from high-palaeolatitude (about 55° S) early Permian-aged (about 280 million years ago) deposits in Namibia that challenges this scenario. *Gaiasia* is represented by several large, semi-articulated skeletons characterized by a weakly ossified skull with a loosely articulated palate dominated by a broad diamond-shaped parasphenoid, a posteriorly projecting occiput, and enlarged, interlocking dentary and coronoid fangs. Phylogenetic analysis resolves *Gaiasia* within the tetrapod stem group as the sister taxon of the Carboniferous Colosteidae from Euramerica. *Gaiasia* is larger than all previously described digited stem tetrapods and provides evidence that continental tetrapods were well established in the cold-temperate latitudes of Gondwana during the final phases of the Carboniferous–Permian deglaciation. This points to a more global distribution of continental tetrapods during the Carboniferous–Permian transition and indicates that previous hypotheses of global tetrapod faunal turnover and dispersal at this time[2,3] must be reconsidered.

The origin and early evolution of digit-bearing tetrapods is marked by two main phases of faunal change: emergence of amniote-dominated dryland faunas in the late Carboniferous[2,3] and replacement of early amniote communities by therapsids in the middle Permian[4]. The fossil evidence for this comes almost exclusively from the densely sampled late Palaeozoic strata of North America and Europe up until the middle Permian, when the locus shifts to higher-latitude faunas in western Gondwana and the temperate latitudes of Laurussia[5,6]. Few exceptions exist: sparse records are known from the Late Devonian to early Carboniferous (Viséan) of Australia[7,8] and the latest Devonian of southern Africa[9], and a diversification of small marine reptiles (mesosaurs) are locally abundant in Brazil, Uruguay and southwestern Africa in the early Permian[10], but these are isolated records that offer limited information about contemporaneous terrestrial faunas. Similar taxa to those of palaeoequatorial Euramerica are known from the Carboniferous–Permian transition of northeastern Brazil[11] and Morocco[12], but these provide little insight into the faunas of higher latitudes comparable to therapsid-dominated faunas of the middle–late Permian.

Here we report a new, exceptionally large, aquatic tetrapod from lacustrine deposits of the lower Permian Gai-As Formation (Huab Basin, northwest Namibia) that provides critical information about the tetrapods that inhabited high latitudes of Gondwana at this time. Its phylogenetic position, in the Tetrapoda stem, relates it more closely to earlier Carboniferous taxa from tropical Laurasia than to tetrapods established in the region later in the Permian. Specimens of the new taxon were recovered in association with scattered fragments of an unidentified tetrapod, possibly a relatively large temnospondyl, fragments of fishes (Osteichthyes and Chondrichthyes), freshwater bivalves and coprolites (Supplementary Information) representing a previously unknown continental vertebrate fauna that lived in high latitudes of Gondwana during the Carboniferous–Permian transition.

Systematic palaeontology

Tetrapoda Jaekel, 1909
Gaiasia jennyae gen. et sp. nov.

Etymology. *Gaiasia* refers to the Gai-As Formation, and *jennyae*, in honour of Jenny Clack (1947–2020) for her landmark accomplishments in the study of early tetrapods.

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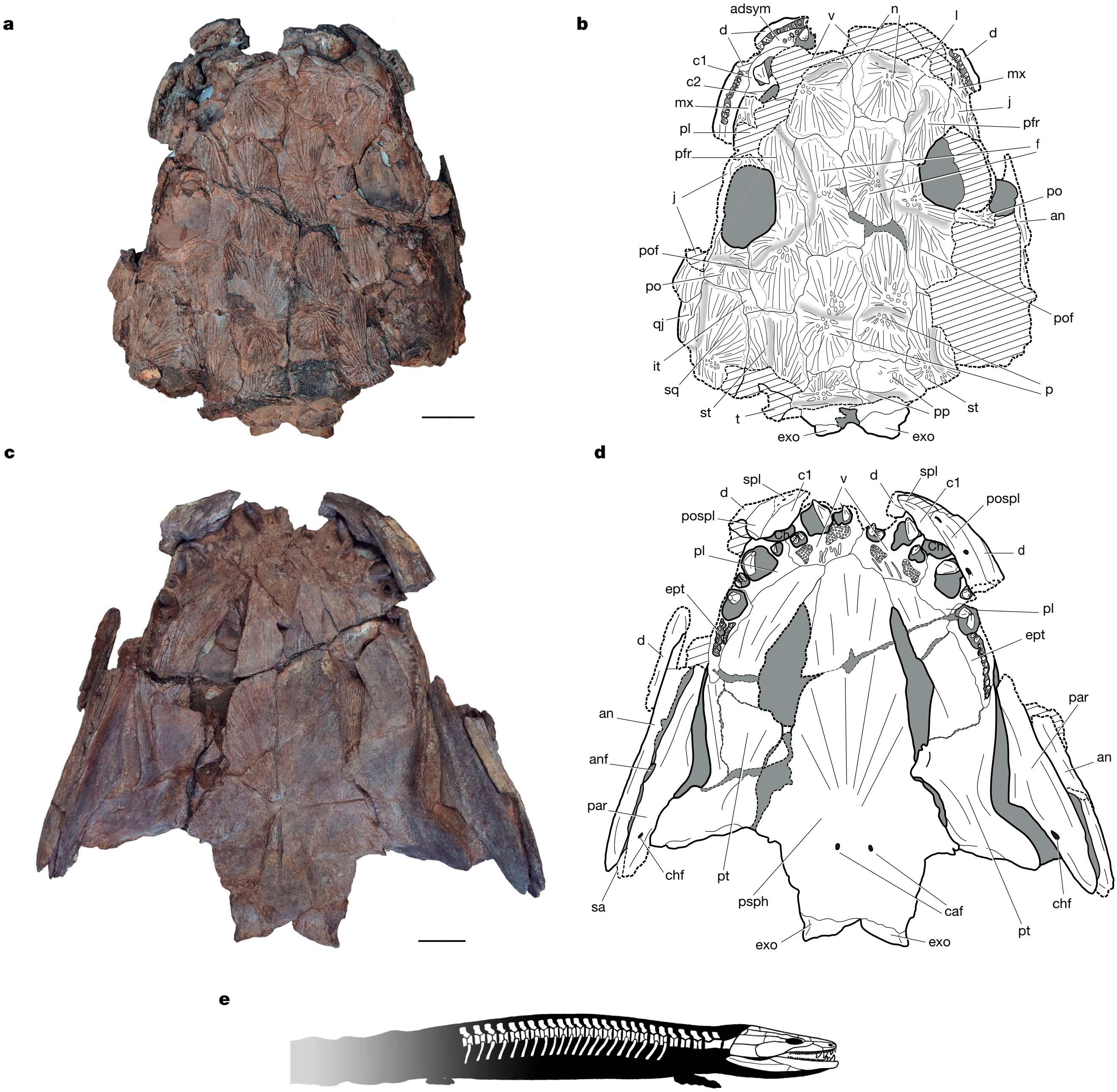

Fig. 1 | *G. jennyae* gen. et sp. nov. (F-1528). a,**b**, Skull in dorsal view. **a**, Photograph. **b**, Interpretative drawing. **c**,**d**, Skull in ventral view. **c**, Photograph. **d**, Interpretative drawing. **e**, Reconstruction of the articulated specimen in lateral view showing preserved elements of the skeleton. adsym, adsymphysial bone; an, angular; anf, angular fenestra; c1, anterior coronoid; c2, middle coronoid; caf, carotid artery foramen; chf, chordatympanic foramen; d, dentary; ept, ectopterygoid; exo, exoccipital; f, frontal; it, intertemporal; j, jugal; l, lacrimal; mx, maxilla; n, nasal; p, parietal; par, prearticular; pfr, prefrontal; pl, palatine; po, postorbital; pof, postfrontal; pp, postparietal; pospl, postsplenial; psph, parasphenoid; pt, pterygoid; qj, quadratojugal; sa, surangular; spl, splenial; sq, squamosal; st, supratemporal; t, tabular; v, vomer. Scale bars, 50 mm (**a**,**c**).

Holotype. Geological Survey of Namibia (National Earth Science Museum) GSN F-1528, a complete skull and mandible articulated with the anterior third of the axial skeleton (Fig. 1a–e and Extended Data Figs. 1–6).

Paratypes. Partial skull including part of the palate, braincase and skull roof (GSN F-1522); anterior half of a palate (GSN F-1504; Supplementary Fig. 1). All of these well-preserved specimens were collected by the authors in the type locality.

Referred material. Skull fragments, including a left palatine and a nearly complete left exoccipital, and series of partially articulated vertebral centra (GSN F-311). This additional material was in the collections of the Geological Survey of Namibia[13] and is here referred to the new taxon.

Remarks. *Gaiasia* is represented by four specimens (holotype, two paratypes and the referred specimen) that include cranial remains, but only the holotype preserves articulated postcranial skeleton. The vertebral column is represented by the atlas and axis plus 24 diplospondylous vertebrae, each composed of a ring-like intercentrum and pleurocentrum of similar size, and articulated ribs. Numerous isolated vertebrae and partially articulated vertebral series have been recovered from the same stratigraphic levels.

Locality and horizon. The locality is referred as north of Doros[13], which is on the northern margin of the Ugab River valley in southern Kunene region, northwestern Namibia (Supplementary Information). Lower third of the Gai-As Formation (Karoo Supergroup), Huab Basin.

The Cisuralian age is based on a U–Pb SHRIMP date (272 ± 1.8 million years ago (Ma), Roadian) of the uppermost beds of the unit[14] and the age of the underlying unit (Artiskian, about 285 Ma)[15,16].

Diagnosis. Distinguishable from all other tetrapods by the unique presence of a wide and flat subtrapezoidal cultriform process of the parasphenoid; interpterygoid vacuities small, elongated and strongly tapered anteriorly; there is a large and a small fang pair on each vomer (the large pair being lateral to the small pair) and each pair comprises one standing fang and a replacement pit; vomerine fangs interlock with similar fangs on the anterior coronoid and those in the symphysis; presence of subdued ornamentation around each skull table bone; skull ornamentation dominated by a ridge-and-furrow pattern; labial surface of the anterior coronoid distinctively bulging with deep fossa accommodating enlarged fang pair.

Description

Although no specimens of *Gaiasia* are complete, most of the skull is present in the holotype or interpretable in the paratypes, as is the anterior axial skeleton. The skull is extremely large, with an estimated basal skull length of approximately 60 cm (from the premaxilla to the tip of the exoccipital condyles). It is broad and flat with a posteriorly extending occiput (Fig. 1 and Extended Data Fig. 6). The skull preserves a generalized tetrapod complement of dermal bones including a small intertemporal. The dermal bones are relatively thin, with simple radiating ornamentation composed by ridges and furrows that radiate from the centre of each bone; this pattern is primarily seen in some Carboniferous taxa[17] and in juvenile temnospondyls[18]. Sutural contacts are weakly developed and largely consist of broadly overlapping scarf joints with minimal interdigitation. A pineal foramen is absent between the parietals; closure of the pineal foramen during ontogeny has been reported in some basal temnospondyls[19,20]. Lateral line canals are present across the skull as open sulci. The orbits are trapezoidal in shape and are widest along the lateral margin, where the angles of the orbit incise into the jugal. Trapezoidal or irregularly shaped orbits are observed in a wide array of stem tetrapods, notably the whatcheeriids[21,22] and some embolomeres[23].

The skull roof consists of a relatively conservative arrangement of dermal bones with a few notable exceptions. The frontals have an S-shaped contact with the nasals, projecting weakly between them but to a substantially lesser extent than that observed in colosteids[24]. The nasolacrimal region is poorly preserved but includes an infraorbital process of the jugal and a slender anteroposteriorly elongated prefrontal. Parts of a lacrimal may be present with small participation in the orbital margin. In contrast with that of many stem tetrapods, the postfrontal is a large anteroposteriorly elongated bone. A small intertemporal is present but is excluded from contact with the parietal by a temporal process of the postfrontal, an arrangement possibly unique to *Gaiasia*.

The palate is distinctive among early tetrapods (Fig. 1 and Extended Data Fig. 6). The parasphenoid is a massive diamond-shaped bone that makes up most of the palatal surface. It is flanked by narrow elongate pterygoids that suture broadly with the vomer and the parasphenoid, thus forming a slit-like interpterygoid vacuity, a condition relatively rare among early tetrapods with the exception of adelospondyls[25]. All marginal bones of the palate hold massive tusks that tightly interlock with the corresponding tusks on the mandibular symphysis and the anterior coronoids.

The occiput preserves distinctive features of the atlantooccipital joint, spiracular cleft and occipital vascular organization (Extended Data Figs. 1, 2 and 6). The occipital arch is dominated by paired articular surfaces of the exoccipital, which form a hinge-like articulation with an unusual ventrally fused atlas–axis complex. Such an arrangement of the atlantooccipital articulation is reminiscent of that seen in keraterpetontids[26], recumbirostrans[27], stereospondyls[28] and lissamphibians[29] but differs from these in the presence of an elongate but medially restricted basioccipital that appears to enclose a notochordal remnant. A broad paired ossification in the supraoccipital region is present posterior to a massive medial extension of the opisthotic (Extended Data Figs. 1 and 2a,b). The spiracular cleft is marked by a wide shallow excavation in the temporal region. This excavation is bisected by a process of the opisthotic, separating the spiracular cleft (medial) from the recess accommodating the depressor mandibulae (lateral), similar to the organization of this region in many stem tetrapods[30].

The lower jaw has a relatively parabolic shallow profile, coincident with the palatal tooth arch, and posteriorly, it deepens at the level of the suspensorium (Fig. 1 and Extended Data Fig. 3). The mandible extends behind the glenoid in a postglenoid area. As in colosteids, enlarged fang pairs are present on the dentary symphysis (one on the adsymphyseal ossification and the other on the dentary as part of the marginal tooth row) and on the anterior coronoid[31], which forms in *Gaiasia* a lingually rounded prominence with a deep fossa accommodating the fang. No Meckelian foramina are visible. The angular and prearticular articulate along a simple butt joint along the ventral surface of the jaw, thus concealing the Meckelian bone and without a lingual exposure of the angular (mesial lamina). The absence of lingual exposure of the angular is commonly observed in Devonian and early Carboniferous tetrapods[31] but nearly all later tetrapods present a mesial lamina of the angular[31,32]. At the ventral contact between the angular and prearticular there is a slit-like foramen at the level of the glenoid; a similar foramen has been identified in colosteids as the angular foramen[31]. The postglenoid area is composed solely of contributions from the prearticular and angular, extending directly posteriorly and tapering to a point, and concealing the articular. Dorsally and labially, the surangular also extends onto the postglenoid area but without contacting the prearticular; this has been considered a primitive condition for tetrapods present in most Devonian taxa[32]. Between the lower jaws and ventral to the parasphenoid, a well-ossified ventromedial bone of the branchial arches was found in life position during preparation of the specimen (Extended Data Fig. 4). This element is nearly straight, exhibits a prominent ventral keel and is forked anteriorly. This element compares well with both the urohyal of *Tiktaalik*[33] and the basibranchial of the colosteid *Greererpeton*[34]. No ossified ceratobranchials are present.

An articulated anterior axial skeleton is preserved in the holotype (Extended Data Fig. 5). The centra of the atlas–axis complex are fused ventrally into one element with separate arches. A large oval foramen pierces the ventral surface of the atlas–axis complex. All posterior vertebral centra are diplospondylous. Neural spines are low and rectangular in transverse section, with broad pedicels and prominent rectangular parapophyses, similar to the condition in *Greererpeton*. In some specimens, the tops of the neural spines exhibit irregularly surfaced bone. Ribs are robust and extend laterally from the parapophyses. The distal ends of the ribs form a cortical collar surrounding rough-textured bone, indicating a substantial cartilaginous terminus to each rib. No bones of the appendicular skeleton (including girdles) have been identified thus far, which is particularly remarkable as several specimens are known and some preserved articulated within calcareous nodules (Supplementary Information). It is possible that the limb and girdle bones were reduced or lost in life.

Phylogenetic relationships

To evaluate the phylogenetic position of *Gaiasia* in the context of the early diversification of Tetrapoda and its closest relatives, we constructed a new comprehensive data matrix of early tetrapods including the tetrapod stem group as well as Palaeozoic and Triassic representatives of the amniote and lissamphibian lineages. Our results (Fig. 2, Extended Data Fig. 7 and Supplementary Information) are broadly similar to those of recent phylogenetic analyses of early tetrapod relationships[35], with both colosteids and embolomeres resolved stemward of the divergence between temnospondyls (including amphibians) and

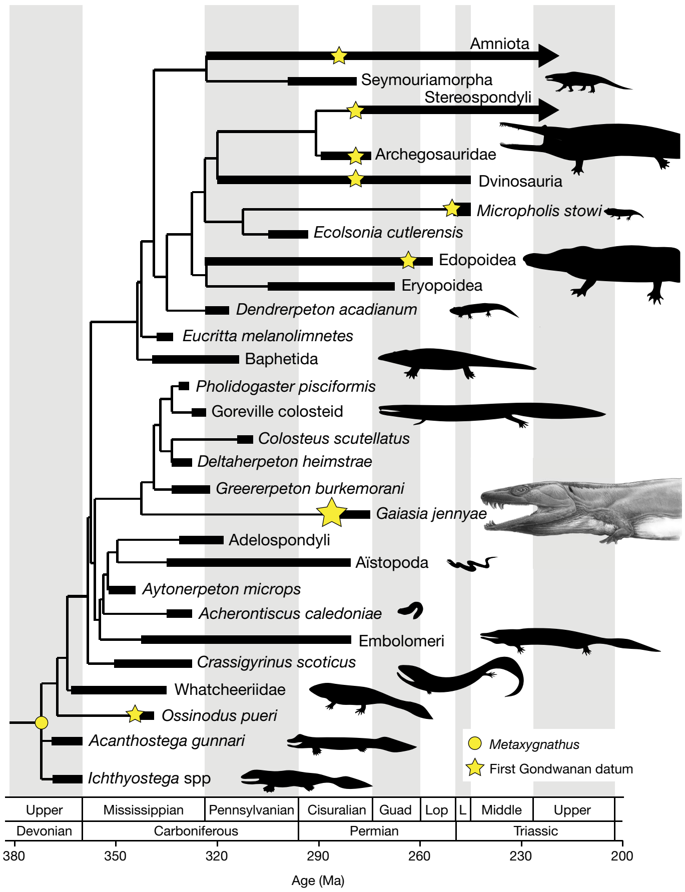

Fig. 2 | Time-calibrated phylogeny (majority-rule consensus tree) of major Palaeozoic and Triassic tetrapod lineages illustrating the relationships of *G. jennyae* and the evolution of body size. Body size silhouettes are scaled relative to each other and represent the largest specimen known for each clade, except for Amniota. See Extended Data Fig. 7 and Supplementary Information for details on phylogenetic analysis and Supplementary Tables 1 and 2 for first occurrences of higher clades. Guad, Guadalupian; Lop, Lopingian; L, Lower. Silhouettes are reproduced from ref. 35, Springer Nature Limited. Illustration of *G. jennyae* by G. Lio.

amniotes. We recover *G. jennyae* as the sister taxon to a monophyletic Colosteidae, here encompassing the Carboniferous *Greererpeton*, *Deltaherpeton*, *Colosteus*, *Pholidogaster*, and the unnamed Carboniferous Goreville colosteid. We find the clade *Gaiasia* + Colosteidae outside the tetrapod crown-group, within a paraphyletic array of early tetrapods that appeared in palaeoequatorial Euramerica by the Mississippian (early Carboniferous; Fig. 3). This topology implies a divergence between *Gaiasia* and Colosteidae by the Viséan (about 330 Ma), the time of the first occurrence of the earliest colosteids in North America. The fact that colosteids disappear from the Euramerican record by the end of the Moscovian (about 307 Ma) and the absence of *Gaiasia*-like tetrapods in the well-sampled Euramerican faunas of Carboniferous–Permian transition age suggest that there was interchange between Euramerican and high-latitude Gondwanan tetrapod communities before completion of Gondwanan deglaciation at the Carboniferous–Permian transition[36].

Gaiasia preserves anatomical traits from the braincase, palate and lower jaw broadly consistent with its placement within this early Carboniferous diversification of basal tetrapods. A close relationship with the Colosteidae is supported by the presence of a prominent fang on the first coronoid but absence on the second coronoid, as well as presence of an angular foramen in the ventral border of the mandible; nevertheless, when included in a phylogenic analysis, *Gaiasia* seems to fall outside the Euramerican Colosteidae. The *Gaiasia* + Colosteidae clade is recovered on the tetrapod stem, crownward to Devonian and Mississippian 'whatcheeriids' but stemward to baphetids and *Eucritta* (Fig. 2). This position is supported by the poorly demarcated epipterygoid, presence of fangs on the anterior coronoid, and a prominent occipital foramen serving the occipital artery. Conversely, we find no close relationship between *Gaiasia* and other tetrapods from the Palaeozoic of Gondwana, such as the Australian 'whatcheeriid' *Ossinodus*[8] and various temnospondyl lineages, including dvinosaurs, edopoids and stereospondylomorphs, most of which appear in Gondwana at lower palaeolatitudes before the end of the early Permian[11].

Discussion

Our discovery and identification of a giant stem tetrapod from the lower Permian of Namibia greatly expands our understanding of the morphology, ecology and biogeography of the initial diversification of tetrapods. The phylogenetic position of *Gaiasia*, as the sister taxon of Colosteidae within the tetrapod stem, is well supported by characters of the braincase, mandible and palate. *Gaiasia* is unique among digited stem tetrapods in its large size and geographic occurrence, representing an ecologically important apex predator of a new high-latitude Gondwanan fauna.

Gaiasia is the largest digited stem tetrapod known at present with a basal skull length of approximately 60 cm (Fig. 2). Digit-bearing stem tetrapods in equatorial Laurussia are generally much smaller, with the largest representatives achieving basal skull lengths of between 30 and 40 cm. The Devonian tetrapod footprint record suggests the presence of large stem tetrapods, although still smaller than *Gaiasia*[37]. Wide flat parabolic skulls such as that of *Gaiasia* are associated with suction feeding in an aquatic environment[38], an inference also supported by strain-limiting adaptations in the atlantooccipital system (such as the posteriorly projecting occiput and sutured atlas–axis complex) and adaptations for branchial depression (such as the well-ossified basibranchial). However, the large interlocking coronoid and palatal fangs suggest that feeding in *Gaiasia* also entailed a powerful bite during physical capture of large prey. Some unique features of *Gaiasia*, such as the structure of the posteriorly oriented spiracular chamber and the massive diamond-shaped parasphenoid, might be consequences of its unique flattened skull morphology.

As the largest Palaeozoic suction-feeding tetrapod, *Gaiasia* demonstrates that digited stem tetrapods were not intrinsically excluded from the apex freshwater predator niche. We suggest that size limits on stem tetrapods in Euramerica and in lower-latitude Gondwana may have been a consequence of competitive exclusion from this niche at lower latitudes, perhaps by large fishes in the Carboniferous, and by large temnospondyl amphibians in the early Permian. It is also possible that the exceptional large body size of *Gaiasia* may reflect thermophysiological constraints or releases associated with cold-temperate climates in alignment with Bergmann's rule[39], indicating new directions for inquiry into early tetrapod physiology. Regardless, our new data strongly suggest that important adaptations in the early radiation of tetrapods took place outside the well-sampled basins of palaeoequatorial Pangaea.

Our findings also suggest a more complex scenario regarding diversification dynamics and community assembly in early tetrapod faunas through the end of the early Permian. Quantitative analyses have forwarded mechanistic explanations for patterns of tetrapod diversification[40] and extinction[41,42] throughout the late Palaeozoic, but these analyses draw primarily on well-sampled palaeoequatorial basins of North America and Europe (Fig. 3). The record of early tetrapods outside these basins is poor, with only a handful of isolated specimens described[7–10,20]. Recent work has begun to reveal tetrapod associations from northern Gondwana[11,12,43], but quantitative studies have generally interpreted these as variations of the palaeoequatorial

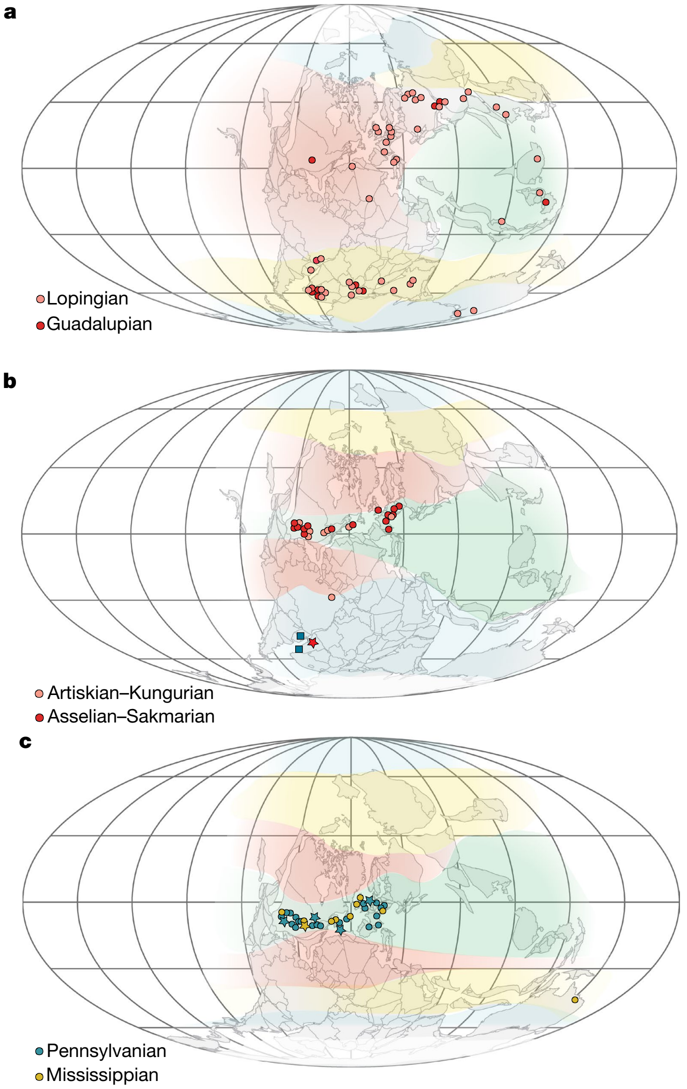

Fig. 3 | Palaeogeographic reconstructions of Pangea from Permian to Carboniferous with the dominant palaeoclimatic belts. On each reconstruction, the distribution of the tetrapod fossil-bearing sequences (basins) in Pangea is indicated and based on the database of ref. 2. The plate configuration and palaeoclimatic reconstructions are based on ref. 49; white, cold belt; blue, cool temperate belt; yellow, arid belt; green, tropical belt; red, warm temperate belt. **a**, Middle Permian reconstruction showing the distribution of Guadalupian (middle Permian) and Lopinginan (late Permian) fossil-bearing sequences. **b**, Early Permian (Cisuralian) reconstruction with the early Cisuralian fossil-bearing sequences (Asselian–Sakmarian) differentiated from the late Cisuralian ones (Artiskian–Kungurian). Southern Gondwanan late Cisuralian mesosaur-bearing sequences and the Huab Basin are indicated as blue squares and a red star, respectively. **c**, Carboniferous reconstruction showing the distribution of Mississippian (early Carboniferous) and Pennsylvanian (late Carboniferous) basins with colosteid-bearing sequences indicated with a star.

faunas[42]. However, there are some indications that important aspects of tetrapod diversification (such as the sudden appearance of some important lineages of palaeoequatorial tetrapods without obvious antecedents) are obscured by this restricted spatial sampling[5,44]. We suggest that this may have been a consequence of immigration from outside Laurussia rather than in situ evolution of these groups[5,6]; thus, sampling from regions such as southern Gondwana may change the reconstruction of early tetrapod diversity dynamics. The importance of southern continents in early tetrapod evolution has largely been dismissed on the basis that the region was rendered uninhabitable through the early Permian by widespread and protracted glaciation, even at lower latitudes[45,46]. However, recent work shows that this glacial interval consisted of numerous small ice centres that waxed and waned diachronously across southern Gondwana[47], with floral composition indicating prevalence of milder climate at high latitudes[35]. The presence of an extremely large freshwater tetrapod in the lower Permian of the Huab Basin suggests the existence of stable continental tetrapod communities at high latitudes (about 55° S; Fig. 3) through the final phases of the Palaeozoic Gondwanan glaciation. This is further indicated by abundant amniote trackways from the earliest Permian (Asselian) of southern South America[48] and undescribed fish and tetrapod material from the Gai-As Formation (Supplementary Information). As these higher latitudes may have been insulated from events such as the Carboniferous rainforest collapse[2,3], other novel lineages such as that represented by *Gaiasia* may exist and may markedly change reconstructions of global diversification and extinction dynamics.

Our finding of a unique fauna in cold-temperate Gondwana shows that high-latitude faunas in the Carboniferous–Permian transition were not equivalent to well-sampled palaeoequatorial communities. We propose that previously postulated global biodiversity changes (extinctions) at the Cisuralian–Guadalupian (early–middle Permian) transition[41,42] might instead reflect a shift in sampling of terrestrial fossil tetrapods from tropical to temperate regions of Pangaea[5] (Fig. 3). Further, late Palaeozoic global ecological megatrends, such as extirpation of wetland faunas[3] and the west–east expansion of dryland-adapted tetrapod faunas[2], should be interpreted with caution, as they may relate only to the tropical equatorial zone of Pangaea. We expect more exhaustive sampling of southern high-latitude temperate zone faunas across the Carboniferous–Permian transition, of which *Gaiasia* is a part, to reveal previously unrecognized spatial and temporal patterns of tetrapod palaeodiversity across the supercontinent at the end of the great late Palaeozoic Gondwanan glaciation.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-024-07572-0.

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Methods

Phylogenetic analysis

We carried out a phylogenetic analysis to test the affinities of *G. jennyae* in the context of the interrelationships of early tetrapods, including basal members of the amniote and amphibian lineages. A new dataset was constructed using a combination of characters from previous comprehensive analyses on basal tetrapods, some of them modified, and new characters produced during the present work (character list and data matrix as a Nexus-formatted file in Supplementary Information). The resultant data matrix of 217 characters and 59 taxa was analysed using PAUP*4.10a (ref. 50). We conducted six heuristic searches, one unweighted and five using implied weighting. The heuristic search strategies started from 10,000 random addition sequences, automatically increasing the number of trees held at each step and applying the TBR algorithm in PAUP. All characters were considered as non-additive and unordered. We applied DELTRAN optimization and treated multistate characters as variable to distinguish ambiguities from polymorphisms. Outgroup was specified to include *Acanthostega gunnari* and *Ichthyostega* spp. The implied weight analyses were carried out with concavity constants (K)[51] using successive values (2, 4, 6, 8 and 10). The analysis with equally weighted characters found four most parsimonious trees of 1,689 steps with a consistency index of 0.1658 and a retention index of 0.4776, which were summarized using a strict consensus (Extended Data Fig. 7). Figures were produced using Adobe Photoshop 24.3.0 and Adobe Illustrator 27.4.1.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The authors declare that all the data supporting the findings of this study are available within the paper and the Supplementary Information. All nomenclatural acts are registered with ZooBank (https://zoobank.org) under the Life Science Identifier urn:lsid:zoobank.org:pub:62D1B947-D36F-49D2-8490-EAD49C46A22B.

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Author contributions The project was conceived by C.A.M., R.M.H.S. and J.D.P.; phylogenetic analysis was carried out by C.A.M. and J.D.P.; R.M.H.S., C.A.M., A.C.M., L.C.G. and H.M. conducted fieldwork to collect specimens and geological context. C.A.M., J.D.P. and R.M.H.S. wrote the manuscript, with comments from all authors.

Competing interests The authors declare no competing interests.

Additional information

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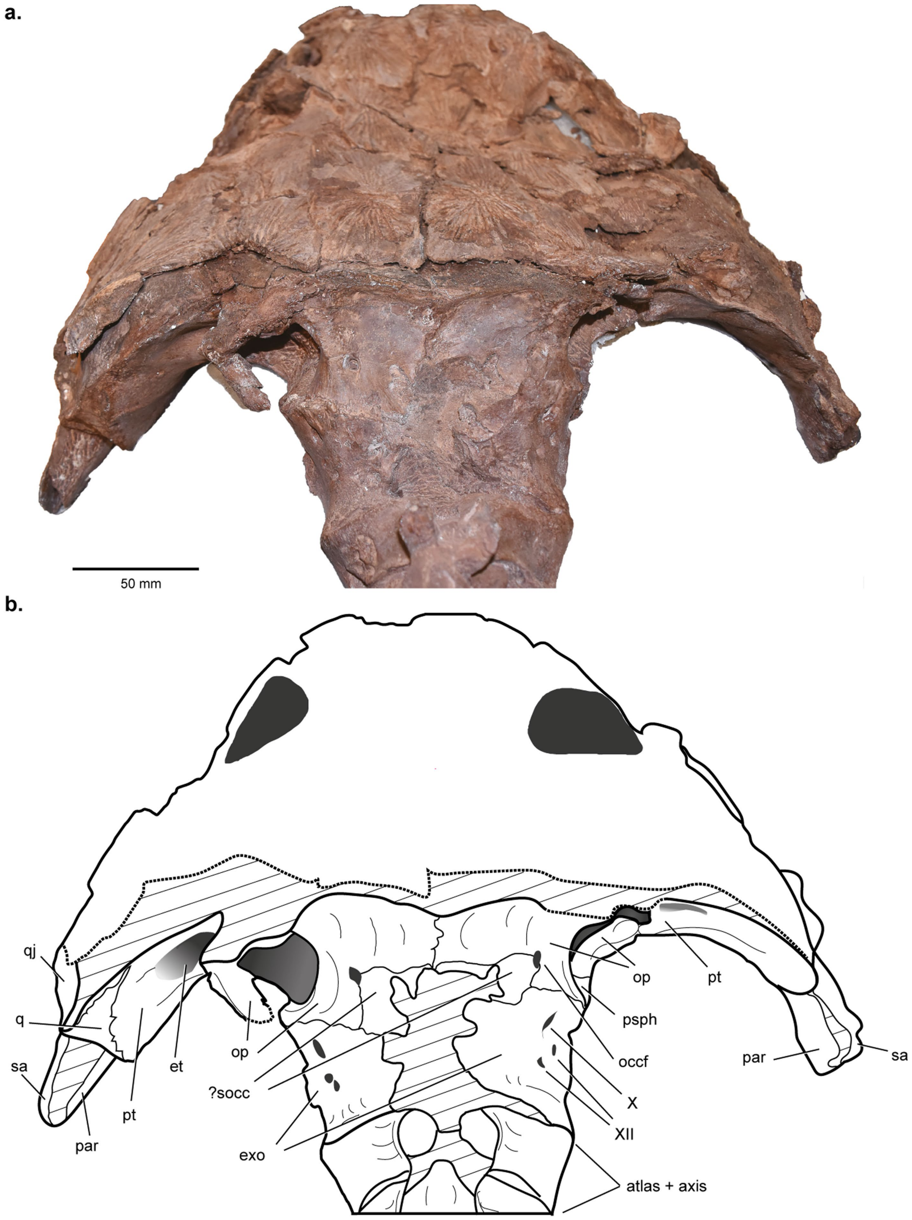
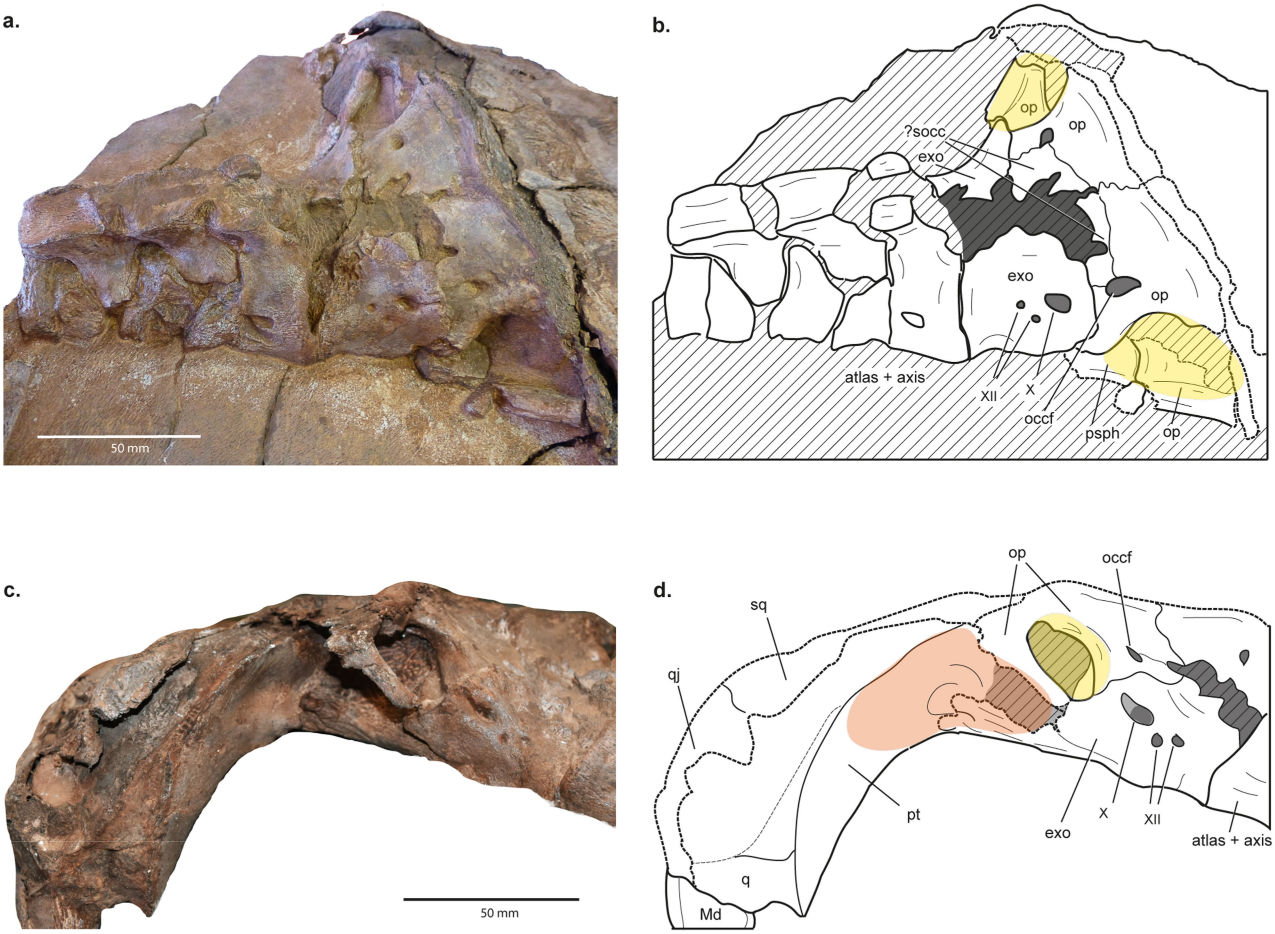
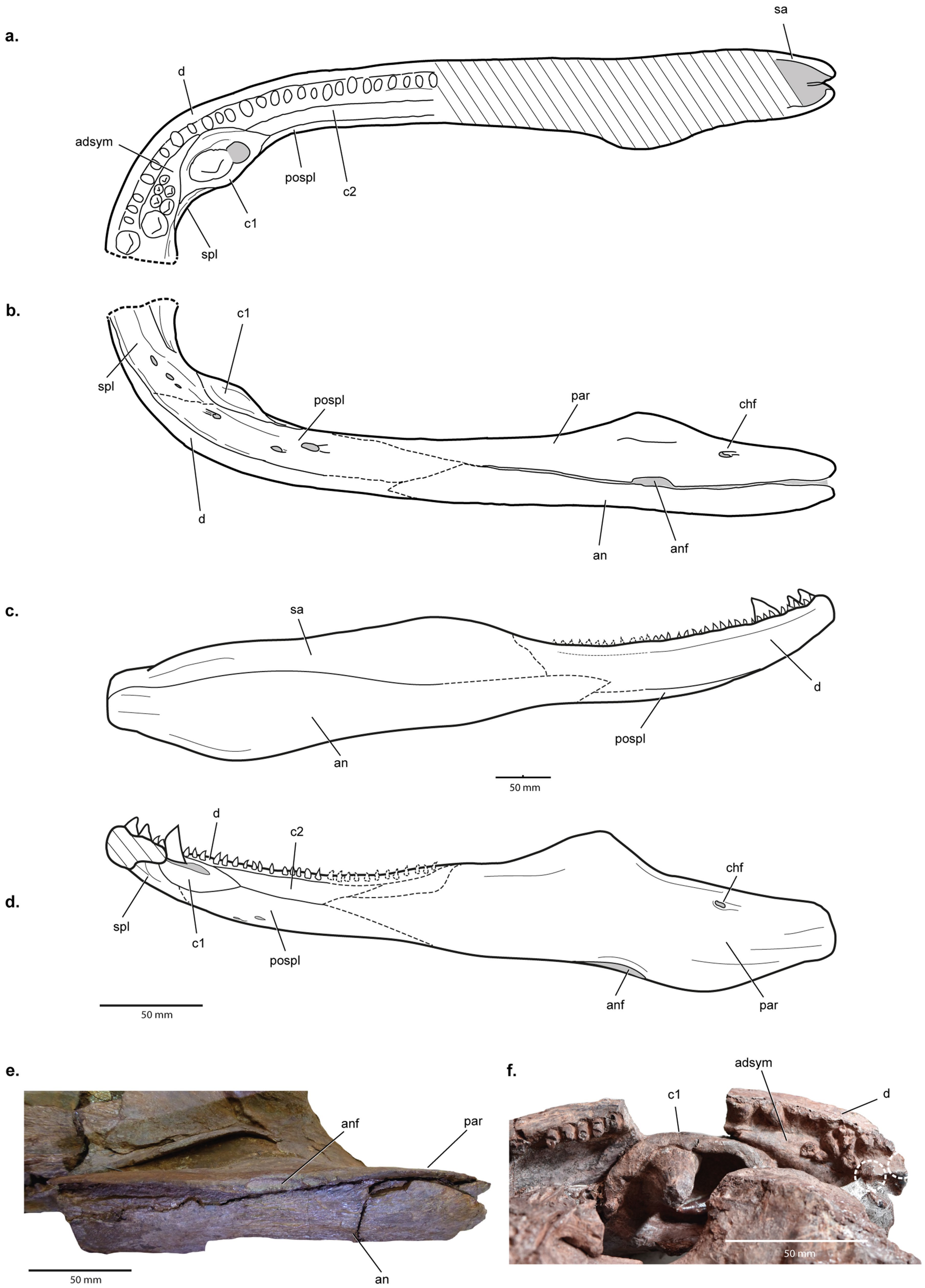


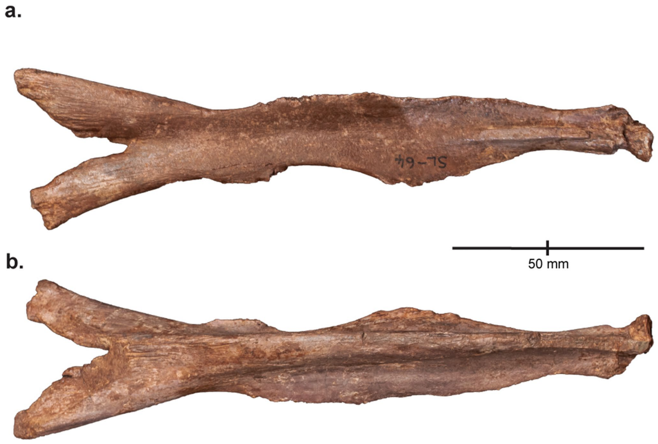
Extended Data Fig. 1 | *Gaiasia jennyae* gen. et sp. nov. (F-1528). a,**b**, skull in posterior view. **a**, Photograph. **b**, Interpretative drawing. Scale bar, 50 mm. et, *excavatio tympanica*; exo, exoccipital; occf, occipital artery foramen; op, opisthotic; par, prearticular; psph, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; sa, surangular; ?socc, supraoccipital; X, XII, cranial nerves X and XII, respectively.



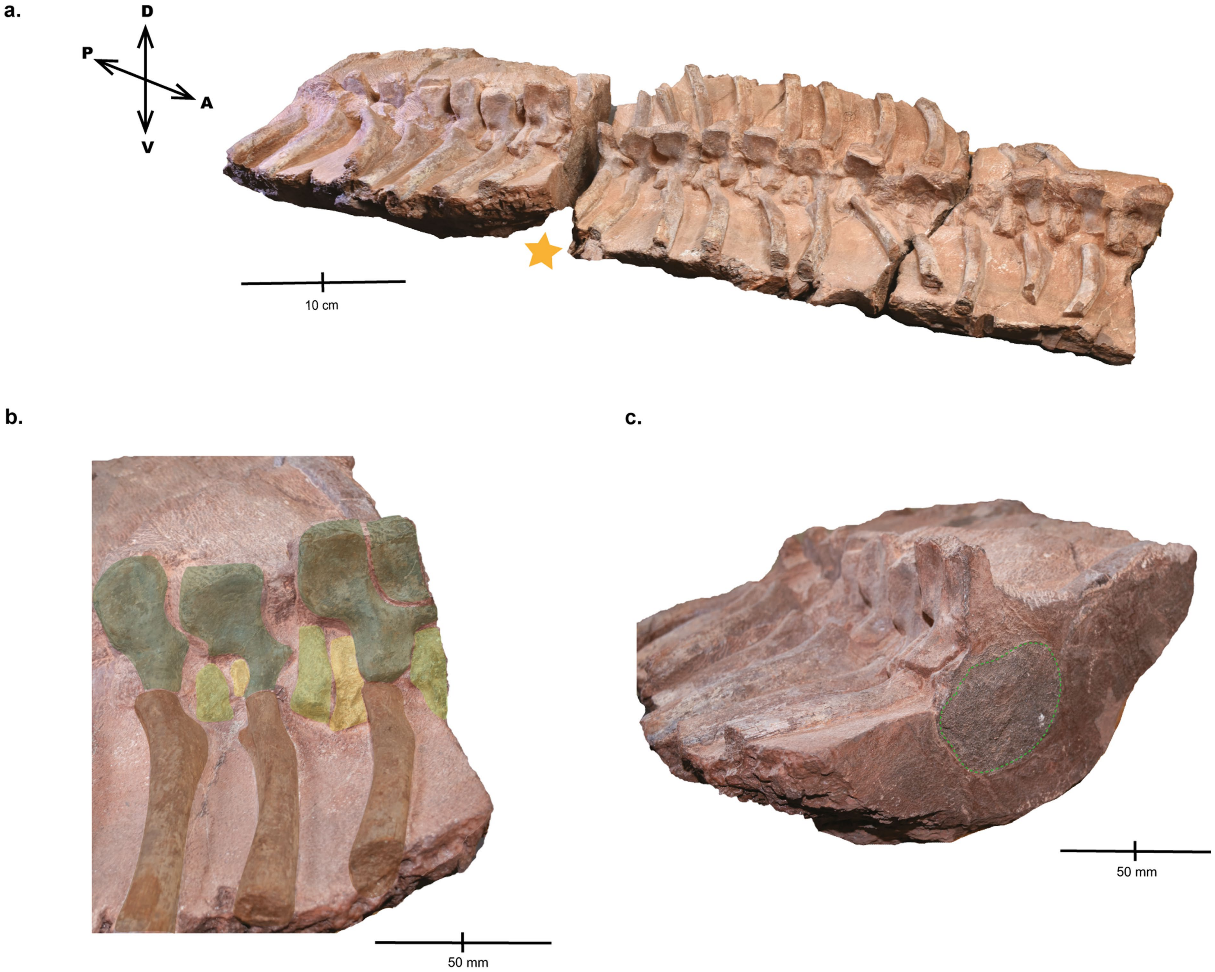
Extended Data Fig. 2 | *Gaiasia jennyae* gen. et sp. nov. (F-1528). a,**b**, Right lateral view of the posterior part of the skull and anterior vertebrae during preparation of the specimen. **a**, Photograph. **b**, Interpretative drawing. **c**,**d**, Posterior view of the left side of the skull. **c**, Photograph. **d**, Interpretative drawing. Scale bar, 50 mm. exo, exoccipital; Md, mandible; occf, occipital artery foramen; op, opisthotic; psph, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; ?socc, supraoccipital; sq, squamosal; X, XII, cranial nerves X and XII, respectively. Yellow shade, spiracular cleft; red shade, depressor mandibulae; cross-hatching, matrix.



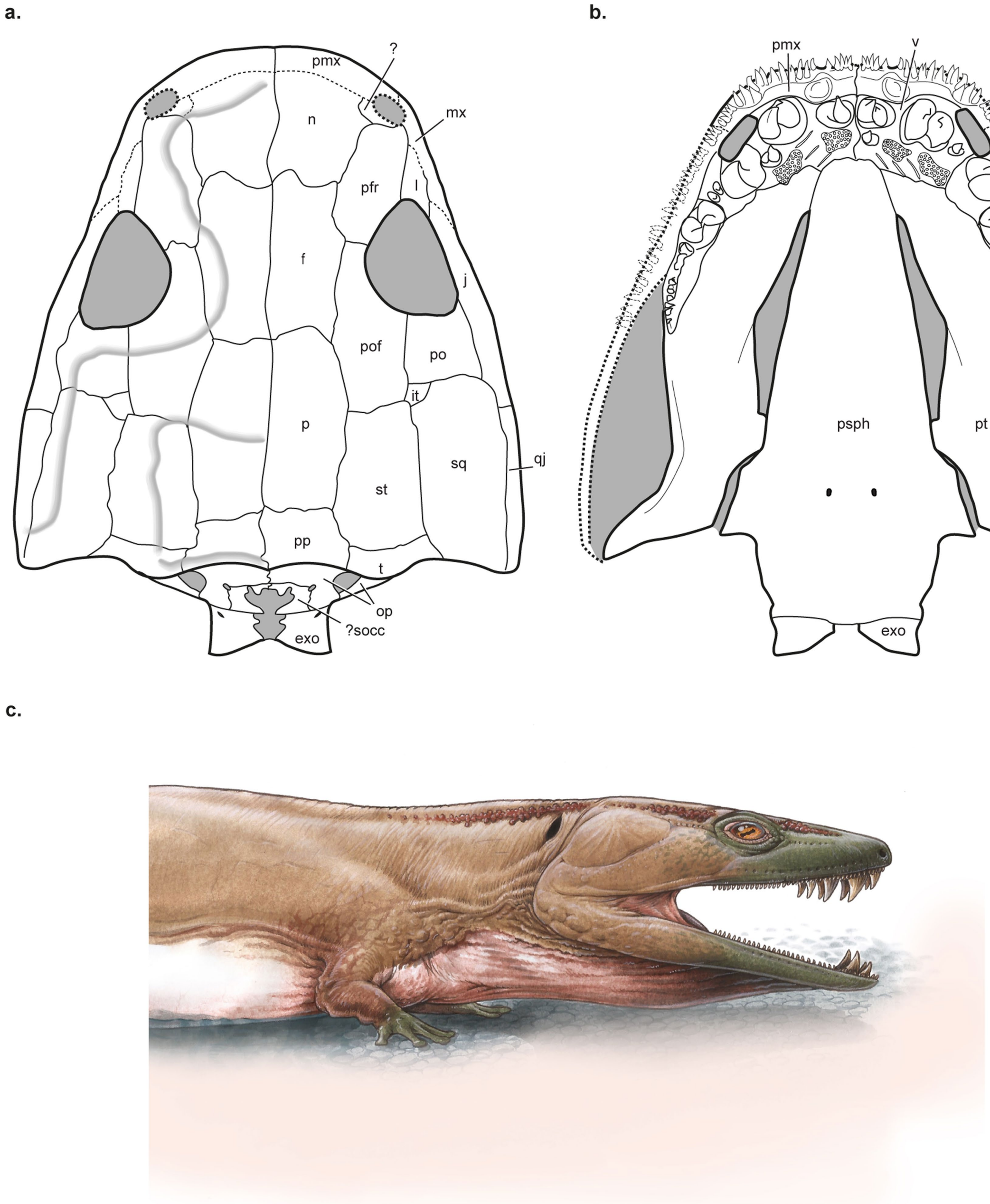
Extended Data Fig. 3 | *Gaiasia jennyae* gen. et sp. nov. (F-1528). a–**d**, Composite reconstruction of the mandible. **a**, Dorsal. **b**, Ventral. **c**, Labial. **d**, Lingual. **e**, **f**. Photographs of the right hemimandible. **e**, Ventral view of the posterior half. **f**, Dorsal view of the symphyseal area. adsym, adsymphysial plate; an, angular; anf, angular fenestra; c1, anterior coronoid; c2, middle coronoid; chf, chordatympanic foramen; d, dentary; par, prearticular; pospl, postsplenial; sa, surangular; spl, splenial. Dotted white circles show the position of the symphysial fangs. Scale bar, 50 mm.



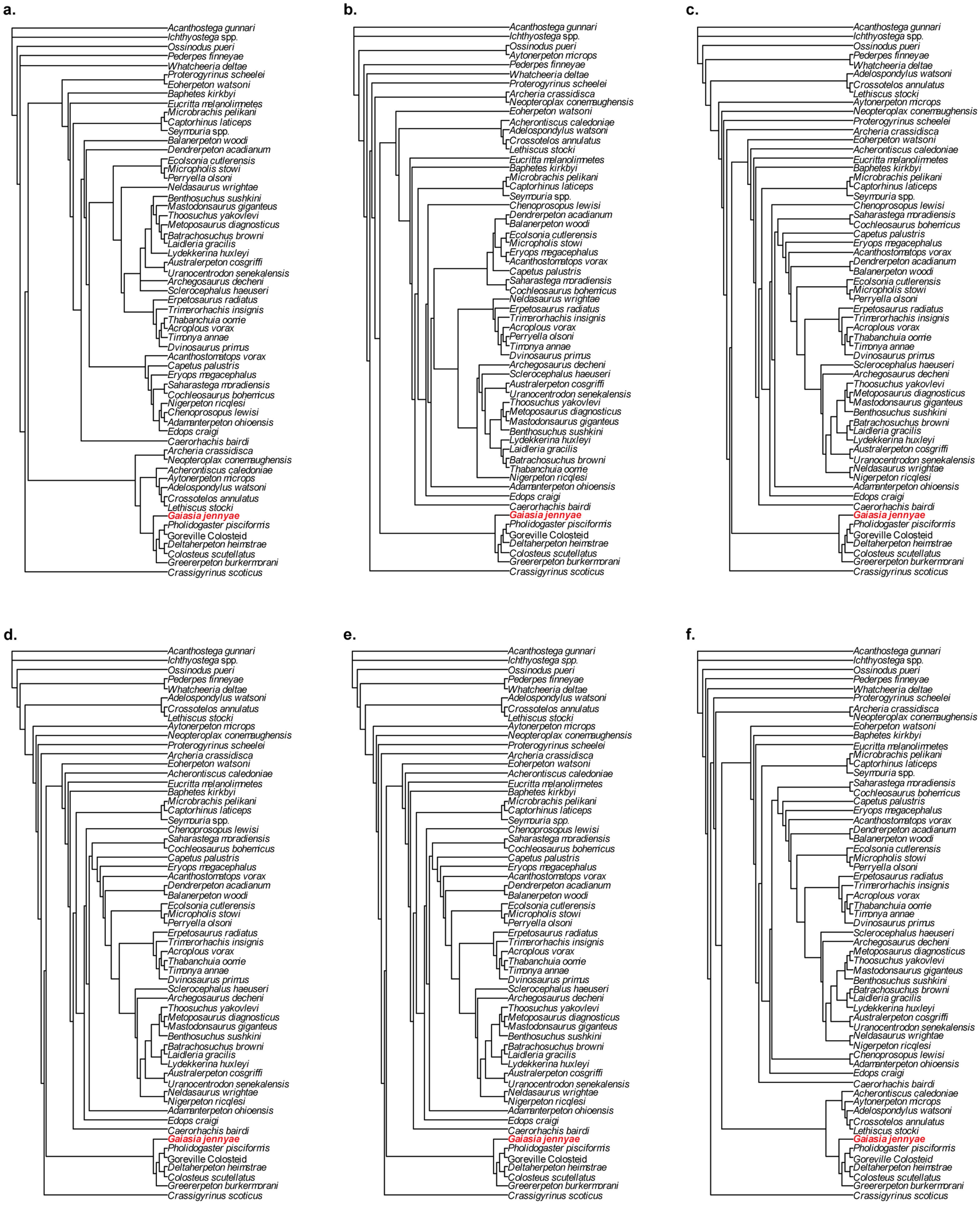
Extended Data Fig. 4 | *Gaiasia jennyae* gen. et sp. nov. (F-1528). Ventral branchial element in **a**, Dorsal and **b**, Ventral views. Anterior to the left. Scale bar, 50 mm.



Extended Data Fig. 5 | *Gaiasia jennyae* gen. et sp. nov. (F-1528). Articulated axial skeleton. **a**, Articulated column in right lateral view. Scale bar, 100 mm. **b**, Detail of the block just behind the star in **a**. Scale bar, 50 mm. **c**, Same block as in **b** in anterior view showing a pleurocentrum. Scale bar, 50 mm. Light green, pleurocentrum; yellow, intercentrum; dark green, neural arch; brown, rib.



Extended Data Fig. 6 | *Gaiasia jennyae* gen. et sp. nov. (F-1528). a–b, Composite reconstruction of the skull. **a**, Dorsal. **b**, Ventral. **c**, Artistic reconstruction of *Gaiasia* in lateral view; artwork by Gabriel Lio. ect, ectopterygoid; exo, exoccipital; f, frontal; it, intertemporal; j, jugal; l, lacrimal; mx, maxilla; n, nasal; op, opisthotic; p, parietal; pfr, prefrontal; pl, palatine; pmx, premaxilla; po, postorbital; pof, postfrontal; pp, postparietal; psph, parasphenoid; pt, pterygoid; qj, quadratojugal; socc?, supraoccipital; sq, squamosal; st, supratemporal; t, tabular; v, vomer. Scale bar, 50 mm.



Extended Data Fig. 7 | Phylogenetic analysis. a, Unweighted strict-consensus tree. **b**–**f**, Strict consensus of trees recovered using implying weights[49]. Implied weights inferred with b, k = 2, c, k = 4, d, k = 6, e, k = 8; f, k = 10.

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Data analysis	The phylogenetic analysis was performed using the phylogenetic software PAUP*4.0a (Swofford, 2003) and the data matrix was compiled in Mesquite (version 3.04).

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Study description	Description of new taxon of a stem tetrapod from the early Permian, represented by several large specimens including a semi-articulated skeleton; a new phylogenetic analysis was perfomed to infer its relationships.
Research sample	Specimens studied are listed in the manuscript (a single holotype specimen, two paratype specimens, and one referred specimen) and represent the currently-known collection of material attributable to this species. All housed in the GNF (Geological Survey of Namibia, National Earth Science Museum).
Sampling strategy	Sample size is limited to the specimens collected in this study.
Data collection	Description of the collecting specimens in the field, and taphonomic and sedimentological data are provided in the Supplementary Information under section 2. Geological setting and taphonomic data.
Timing and spatial scale	Specimens were collected during 2014, 2015, 2019 field seasons. Information on the collecting area and bearing levels are provided in the Supplementary Information under section 2. Geological setting and taphonomic data.
Data exclusions	No data were excluded.
Reproducibility	All data are contained within the manuscript and Supplementary Information file. All parameters for phylogenetic analysis are reported in the Methodology and Supplementary Information under section 3. Character list and phylogenetic datasets.
Randomization	Randomization was not relevant for the study conducted herein.
Blinding	Blinding was not relevant to the anatomical study of the fossils specimens and the phylogenetic analysis performed.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	The field work was done during the southern hemisphere winter season (June-August) in the Huab region of northwestern Namibia, a hyper-arid desert with < 500mm rainfall per year.
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Access & import/export	Geological field work, fossil collecting, and exporting permits to Iziko Museums Cape Town for fossil preparation were done with the

Access & import/export	corresponding permits issued by the Geological Survey of Namibia and the National Heritage Council of Namibia (permits #02/2014 issue 07-08-2014, #09/2015 issue 07-10-2015, and #01/19 issue 05-13-2019)
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Specimen provenance	Geological field work, fossil collecting, and exporting permits to Iziko Museums Cape Town for fossil preparation were done with the corresponding permits issued by the Geological Survey of Namibia and the National Heritage Council of Namibia (permits #02/2014 issue 07-08-2014, #09/2015 issue 07-10-2015, and #01/19 issue 05-13-2019).
Specimen deposition	The holotype, paratypes and referred specimens of Gaiasia jennyae are catalogued and available for study to qualified researchers at GSN (Geological Survey of Namibia, National Earth Science Museum).
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